

Agricultural Fitness of Smooth Bromegrass Populations Selected for Divergent Particle-Size Reduction Index

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ABSTRACT

Voluntary intake potential of a forage crop is generally considered to be the most important feed characteristic regulating animal performance. Efforts to develop forage crops with reduced neutral detergent fiber (NDF) concentration are associated with reduced plant fitness, prompting the development of alternative approaches to improve intake, such as particle-size reduction index (PSRI). The objective of this research was to characterize correlated selection responses of four fitness traits following divergent selection for PSRI. Twelve smooth bromegrass (*Bromus inermis* Leyss.) populations (four base populations and their Cycle-1 high-PSRI and Cycle-1 low-PSRI progeny) were evaluated for forage yield, ground cover, seed yield, and lodging. Divergent selection for PSRI resulted in a negative change in forage yield, ranging from -0.097 to -0.379 Mg ha⁻¹ cycle⁻¹ across the four base populations. Pleiotropy or very tight linkage between loci controlling forage yield and PSRI accounted for only about half of the variation due to selection. The greater inconsistency of forage yield selection responses across the four populations, the lesser proportion of forage yield sum of squares attributable to divergence (pleiotropy or tight linkage), and the reduced magnitude of linear selection responses for PSRI compared to NDF suggest that PSRI may be a more effective selection criterion for improving intake potential of smooth bromegrass.

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Abbreviations: NDF, neutral detergent fiber; PSRI, particle-size reduction index.

PLANT BREEDING EFFORTS to develop forage crops with improved intake potential are increasing (Casler and Vogel, 1999). While there has been considerable effort at making genetic improvements in digestibility (Casler and Vogel, 1999), most ruminant nutritionists consider voluntary intake to be more important than digestibility in limiting animal performance (Fahey and Hussein, 1999). Up to 70% of the variation in animal production can be attributed to variation in intake, while only 20% can be attributed to variation in digestibility (Crampton et al., 1960).

There are two strategies used by breeders to improve intake potential of forage crops. The most common approach is to select for plant traits that decrease bulk volume of feeds. Neutral detergent fiber (NDF) is the most rapid and reliable laboratory predictor of voluntary intake potential of feeds (Mertens, 1994). Physical distension of the rumen is the major factor limiting voluntary intake of high-producing ruminants on high-forage diets (Mertens, 1994). Voluntary intake can be increased by reducing bulk volume of the feed, thereby increasing intake before satiation.

Efforts to breed for increased intake potential of perennial grasses for ruminant livestock, by selection for reduced NDF concentration, have been plagued by persistent reductions in forage yield (Casler, 1999; Han et al., 2001; Surprenant et al., 1988).

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Because NDF is approximately equal to cell-wall concentration (Van Soest, 1994), a positive genetic correlation between NDF and forage yield may be a biological necessity. The plant cell wall represents a physical frame on which numerous plant functions and processes are built. Cell walls are responsible for the retention of upright growth as tillers grow taller, larger, and heavier. Cell walls also function in the transport of nutrients, photosynthate, and water through the vascular system of a tiller. Older phytomers have higher NDF concentrations (Kephart et al., 1990), suggesting an evolutionary adaptation to maintain upright tillers in the grass canopy. These functions of cell walls all allow the plant to continue accumulating dry matter, assuming that no other physiological functions become limiting. The genetic correlations between NDF and forage yield appear to be physiological in origin, caused largely by overlapping genic specificities (i.e., pleiotropy) (Casler, 2005).

An alternative strategy for improving intake potential would be to develop forage crops that have more rapid and/or thorough particle-size breakdown in the rumen of livestock. More rapid particle-size breakdown would increase fiber clearance from the rumen, reducing the time required to stimulate appetite. Voluntary intake of ruminants can be predicted by laboratory measures of breakdown resistance of forages, including particle size distribution following artificial mastication (Troelson and Bigsby, 1964), energy required to grind forages through a given sieve size (Weston, 1985), and energy required to shear or compress forage tissue (Baker et al., 1993). Despite these developments, there has been little effort to utilize these potential selection criteria in forage breeding programs.

The exception is a ball-milling procedure adapted to estimate a particle size reduction index (PSRI) of grass leaves (Casler et al., 1996). The procedure is rapid and repeatable and requires only small amounts of leaf tissue. The PSRI procedure involves a short-term ball milling to break up leaf tissue, followed by sieving over a 1-mm sieve, and determination of the proportion of tissue that passes through the 1-mm sieve. Heritability of PSRI in smooth brome grass (*Bromus inermis* Leyss.) leaves is moderate and rate of genetic gain has averaged 2 to 6% per cycle of selection (Culvenor and Casler, 1999). The objective of this study was to identify changes in agricultural fitness traits (forage yield, ground cover, seed yield, and lodging) associated with divergent selection for PSRI in four populations of smooth brome grass.

MATERIALS AND METHODS

Germplasm and Selection History

Phenotypic selection was applied to four smooth brome grass populations: the cultivars Alpha and Lincoln, and the synthetic populations WB19e and WB88S-Alt (Falkner and Casler, 1998). Cycle-1 high-PSRI and low-PSRI progeny populations were

created in each base population. The selection protocol was described in detail by Casler (2002). Direct selection responses to divergent selection for PSRI concentration were fairly consistent across populations (1.9 to 3.9% units cycle⁻¹), were highly linear, and were all significant at $P < 0.01$ (Casler, 2002).

Forage Yield Test

The four base populations and the eight selected populations were planted in 0.9 by 3.0 m plots at three locations in April 1997. Locations and soil types were Arlington, WI (43°20' N, 89°23' W; Plano silt loam [fine-silty, mixed, mesic Typic Argiudoll]); Marshfield, WI (44°40' N, 90°10' W; Withee silt loam [fine-loamy, mixed, superactive, frigid Aquic Glossudalf]); and Ashland, WI (46°35' N, 90°54' W; Portwing silt loam [fine, mixed, superactive, frigid Oxyaquic Glossudalf]). The experimental design was a split-plot in randomized complete blocks with four replicates, in which the four base populations were whole plots, and selections (high, original, and low) were subplots. The seeding rate was 21 kg ha⁻¹ on a pure live seed basis. Germination of each population and cycle was determined according to standardized procedures (Association of Official Seed Analysts, 1998). Plots were clipped twice during the establishment year and fertilized with 56 kg N ha⁻¹.

Plots were harvested with a flail harvester three times per year in 1998 through 2000, generally in early June, early August, and October. Each location was fertilized with 90 kg N ha⁻¹ in early spring and following each of the first two harvests of each year. A random 500-g sample was collected from the harvested forage of each plot and dried at 60°C for dry matter determination. Forage yield was summed over harvests within each year before any statistical analysis. Survival of each plot was determined by visually rating ground cover following the first harvest of 2000, using a frequency grid (Vogel and Masters, 2001).

Seed Yield Test

Seedlings of each population were raised for 12 wk in the greenhouse before transplanting to the field in May 1997. Seed yield tests were transplanted adjacent to each of the three forage yield tests (Arlington, Marshfield, and Ashland). Each plot consisted of a row of 15 seedlings, spaced 0.3 m apart within rows and 0.9 m apart between rows. The experimental design was identical to that used for the forage yield test, with the exception that three replicates were used. Plants were clipped and fertilized as described for the forage yield test during the establishment year.

By May 1998, adjacent plants within rows had tillered sufficiently to form nearly continuous rows at Marshfield. Plots were fertilized with 56 kg N ha⁻¹ in early spring 1998 and 1999. Seed ripening was determined when most peduncles were yellowed to the flag-leaf node, the date of which did not vary among populations or cycles. Each plot was scored for lodging percentage averaged across all plants (e.g., 0 = all plants fully vertical; 50 = all tillers of all plants at a 45° angle, half of the plants vertical and half flat on the ground, or some variation thereof; and 100 = all plants flat on the ground). All seed was harvested in bulk from each plot, dried at 30 to 45°C for several weeks, threshed, cleaned, and weighed. Threshing and cleaning was done by one person to avoid differences due to technique. Seed yield tests were treated with pre-emergence

herbicides for weed and volunteer seedling control as described by Falkner and Casler (1998). The seed yield tests at Arlington and Ashland were allowed an additional year for establishment. Rows were continuous by spring 1999 and seed was harvested in 1999 and 2000.

Statistical Analysis

Forage yield, survival, seed yield, and lodging were analyzed by conventional analysis of variance, nearest neighbor analysis, or trend analysis (Casler, 1999) for each location-year combination. The best model was chosen based on the lowest average variance of a treatment mean (Brownie et al., 1993). The data for each location-year were reanalyzed using only the spatial terms in the best model (excluding all treatment effects) and the residuals were saved. The experiment mean was added to each residual so that they represented the original data adjusted to eliminate the spatial variation accounted for by either the nearest neighbor or trend analysis model (Smith and Casler, 2004).

Adjusted values for forage yield, survival, seed yield, and lodging were each analyzed by analysis of variance using the split-plot-in-time model (Steel et al., 1996). Degrees of freedom in these models were subtracted from pooled experimental errors, according to the number of parameters fit in the spatial models for each location-year combination (Casler, 1999). Experimental error mean squares and all *F*-tests were recomputed in a spreadsheet after adjustment of error degrees of freedom. All effects were fixed, except replicates, which were assumed to be random.

Degrees of freedom for the 12 populations were partitioned as follows in the analyses of variance: base populations (3 df), divergence (1 df), populations \times divergence (3 df), asymmetry (1 df), and asymmetry \times divergence (3 df). Divergence was defined statistically as the difference between means of the C+1 and C-1 populations. Asymmetry was defined statistically as the difference between the mean of C0 and the mean of C+1 and C-1 populations. The 3 df for populations were ignored and the remaining 8 df were tested by contrasts and their sums of squares were expressed as a percentage of their sum. Divergence equated to pleiotropy or extremely tight linkages that could not be broken during one cycle of recombination (Casler, 2002). Populations \times divergence was equated to linkage, based on the likelihood that populations of divergent ancestry, origin, and genetic segregation patterns have differential linkage disequilibria (Casler, 2002). Asymmetry and populations \times asymmetry were equated to the effects of drift or nonequilibrium allele frequencies (Casler, 2002; Falconer, 1953). The use of only one cycle of selection is a limitation to the precise estimation and separation of pleiotropy and linkage effects, but is intended only to obtain an indication of which phenomenon is more important in controlling the genetic correlation of PSRI with agricultural fitness traits.

RESULTS AND DISCUSSION

Population \times location, population \times year, and population \times location \times year interactions were not significant for survival, seed yield, and lodging. These interactions were all significant for

forage yield ($P < 0.05$), but these interactions were all due to changes in magnitude of correlated selection responses, not to rank changes among cycle means or to differential direction of correlated selection responses. Therefore, all analyses were based on means over locations and years for all four traits. The 12 populations that comprised this study differed in mean values of all four traits across locations and years ($P < 0.01$). Means over selection cycles within the four base populations were significantly different for forage yield, ground cover, and lodging (Table 1). Phenotypic correlation coefficients of PSRI with the four agricultural fitness traits were: $r = -0.76$ ($P < 0.01$) for forage yield, $r = 0.03$ for ground cover, $r = -0.58$ ($P < 0.05$) for seed yield, and $r = -0.11$ for lodging.

The four traits showed four different selection-response patterns (Table 1). Linear divergence was the only significant selection effect for forage yield, accounting for 55.6% of the correlated selection responses for forage yield. This result indicates that linear correlated selection responses among the four populations were not significantly different from each other and can be considered reasonably homogeneous, with heterogeneity among correlated selection responses accounting for only 17.5% of the sum of squares due to selection (Table 1). The simplest genetic explanation for these responses would be that PSRI and forage yield share some common genetic control, either due to pleiotropic loci or tightly linked loci. This was similar to observations of forage yield responses to divergent selection for NDF (Casler, 2005), except that less of the variation in forage yield was explained by selection for PSRI than selection for NDF (56 vs. 72% of the variation due to correlated selection responses). This suggests that shared genetic control over both forage yield and PSRI is considerably less than the shared genetic control over forage yield and NDF observed by Casler (2005). The genetic correlation between PSRI and forage yield is illustrated in Table 2, manifested as correlated changes in forage yield and PSRI across cycles within populations, due to additive genetic variation for these two traits.

Table 1. Mean squares and percentage of the sums of squares attributable to populations, selection effects (divergence and asymmetry), and interactions of selection effects with populations for four smooth bromegrass populations subjected to one cycle of phenotypic selection for divergent particle-size reduction index (PSRI), as measured by four agricultural fitness traits.

Source of variation	df	Forage yield		Ground cover		Seed yield		Lodging	
		MS	%†	MS	%†	MS	%†	MS	%†
Populations (P)	3	14.05**		2249**		33551		369.9*	
Divergence (D)	1	16.39*	55.6	8	0.5	88552*	23.7	13.5	1.6
D \times P	3	1.72	17.5	237	45.6	27915	22.4	179.0	64.8
Asymmetry (A)	1	0.96	3.2	383*	24.6	42801	11.4	98.0	11.8
A \times P	3	2.32	23.6	152	29.2	53030*	42.5	60.2	21.8

*Mean square significant at $P < 0.05$.

**Mean square significant at $P < 0.01$.

†Percentage of total sum of squares for D, D \times P, A, and A \times P (8 df for all selection effects).

Table 2. Means of original populations (C0) and populations selected for divergent particle size reduction index (PSRI; C - 1 = low, C + 1 = high), evaluated at three Wisconsin locations for 3 yr.

Population	Cycle	PSRI	Forage yield	Ground cover	Seed yield	Lodging
			Mg ha ⁻¹	%	kg ha ⁻¹	%
Alpha	C-1	31.7	8.00	74.4	377	17.6
Alpha	C0	34.6	8.00	78.9	343	14.8
Alpha	C+1	35.4	7.81	73.5	360	12.8
WB19e	C-1	27.6	8.07	66.2	307	17.6
WB19e	C0	30.3	8.31	75.2	465	20.2
WB19e	C+1	35.5	7.85	75.2	316	12.3
Lincoln	C-1	34.1	7.72	77.4	402	14.7
Lincoln	C0	36.3	7.66	71.6	301	16.2
Lincoln	C+1	38.8	6.99	71.4	269	17.4
WB88S	C-1	30.7	7.83	55.7	345	18.9
WB88S	C0	35.0	7.11	63.0	349	22.8
WB88S	C+1	37.9	7.07	55.9	255	23.5
LSD _{0.05}		1.6	0.81	8.5	75	8.9

Table 3. Correlated linear responses (divergence), proportion of variation due to selection (R^2), and asymmetry of selection responses for four agricultural fitness traits observed following one cycle of divergent phenotypic selection for particle-size reduction index (PSRI) in four base populations of smooth brome grass, averaged across three locations and 2 yr or 1 yr (ground cover).

Variable/base population	Divergence	P value	R^2	Asymmetry	P value
	Mg ha ⁻¹ cycle ⁻¹			Mg ha ⁻¹	
Forage yield					
Alpha	-0.097	0.63	0.77	-0.091	0.79
WB19e	-0.113	0.58	0.24	-0.344	0.33
Lincoln	-0.365	0.08	0.82	-0.300	0.39
WB88S	-0.379	0.06	0.79	0.336	0.34
Pooled	-0.239	0.02	0.66	-0.100	0.57
Ground cover	% units cycle ⁻¹			%	
Alpha	-0.43	0.83	0.02	-4.94	0.18
WB19e	4.52	0.04	0.75	-4.53	0.22
Lincoln	-3.04	0.16	0.78	2.83	0.44
WB88S	0.08	0.97	0.00	-7.20	0.06
Pooled	0.28	0.79	0.39	-3.46	0.05
Seed yield	kg ha ⁻¹ cycle ⁻¹			kg ha ⁻¹	
Alpha	-15.4	0.42	0.87	10.4	0.75
WB19e	4.6	0.81	0.00	-113.7	<0.01
Lincoln	-55.9	<0.01	0.97	16.5	0.62
WB88S	-23.0	0.23	0.78	-21.2	0.52
Pooled	-22.4	0.02	0.66	-27.0	0.10
Lodging	% units cycle ⁻¹			%	
Alpha	-1.66	0.38	0.98	-0.41	0.90
WB19e	-2.52	0.19	0.51	-4.26	0.20
Lincoln	0.47	0.80	0.16	-1.86	0.57
WB88S	1.47	0.44	0.89	-0.87	0.79
Pooled	-0.56	0.56	0.64	-1.85	0.26

The mean response of forage yield to PSRI selection was -0.24 Mg ha^{-1} ($P = 0.02$), compared to $+0.34 \text{ Mg ha}^{-1}$ ($P < 0.01$) for NDF selection (Table 3; Fig. 1). Only two of the four correlated selection responses were close to significance at the $P = 0.05$ level. These results are in direct contrast to results from divergent selection for NDF in which three of four populations had significant ($P < 0.05$) responses in forage yield. The two selection criteria, PSRI and NDF, are strongly and negatively correlated with each other (Casler, 2002). Hence, the desirable result for increased ruminant intake potential, increased PSRI or decreased NDF, are both associated with reduced forage yield potential. Because these experiments were conducted under conditions identical to those of Casler (2005), the results of the two experiments are directly comparable, indicating that PSRI has substantially less potential to reduce forage yield than NDF as a selection criterion for increased intake potential.

Ground cover differed significantly among the four population groups and the only significant correlated selection response was a uniform asymmetry response across the four populations, although it only accounted for 24.6% of the sum of squares (Table 1). The asymmetry response was represented by a decrease in ground cover in both selected populations, significant as an overall effect but not in any individual base population, although there was no statistical evidence for heterogeneity in this response. Drift is the most logical genetic explanation for this response, resulting in inbreeding and apparent inbreeding depression for ground cover. Asymmetry effects were not observed in the sister populations divergently selected for NDF, reflecting the nature of drift as a phenomenon regulated by random fluctuations in allele frequencies.

Most of the genetic variation in seed yield resulted from divergent selection for PSRI (Table 1), much as was observed for NDF (Casler, 2005). For PSRI, overall divergence and the asymmetry \times population interaction were the only significant effects, accounting for 66% of the sum of squares for seed yield selection responses. Seed yield was reduced by an average of 22.4 kg ha^{-1} , an effect that was statistically homogeneous across the four base populations, although significance could only be detected in one of the four populations (Table 3; Fig. 1). This effect was similar in magnitude to the responses observed for divergent selection for NDF (Casler, 2005). Drift was also a significant factor regulating correlated selection responses for seed yield, accounting for 42.5% of the sum of squares, an effect that was largely expected, because seed yield is highly sensitive to inbreeding depression (Table 3; Fig. 1; Casler, 2005; Hanson and Carnahan, 1956).

Finally, for lodging, there were no significant responses to selection. Observed responses were highly

variable and unpredictable (Table 3; Fig. 1) without any statistical significance observed within or among the four base populations. The four population groups differed in mean lodging, with means ranging from 13 to 18% ($P < 0.05$) indicating that the lack of correlated selection responses for lodging was not due to lack of precision in estimating means and effects, but to lack of segregation, selection pressure, or inbreeding depression for loci regulating lodging responses.

CONCLUSIONS

There is little agreement in the literature as to the relative importance of linkage or pleiotropy as the principal phenomenon causing genetic correlations. Falconer and MacKay (1996) and Simmonds and Smartt (1999) argue that pleiotropy is more important, while Mather and Jinks (1982) argue that linkage is more important. Linkage alone can maintain a large genetic correlation only when linkages are tight and/or the population is highly inbred (Lande, 1984). Simmonds and Smartt (1999) were clearly considering allometric traits when they argued that potential autocorrelations between growth stages and the resulting complexity of living organisms may be caused, directly or indirectly, by pleiotropic loci with overlapping phenotypic specificities. Forage yield and NDF may be considered allometric to a degree, largely because NDF is a significant component of forage yield: $\text{NDF} + \text{NDS} = \text{forage yield}$, where NDS = neutral detergent solubles. It is far less clear that forage yield and PSRI are allometric, largely because mechanistic studies of the PSRI trait have yet to be conducted. This trait has a moderate negative genetic correlation with NDF (Casler, 2002), but it is likely controlled by a number of other plant traits that regulate anatomy, chemistry, and physical properties of smooth brome grass leaves.

Selection for increased intake potential in smooth brome grass, using NDF as the selection criterion, has been problematic, resulting in strong and positive (undesirable) correlated responses for forage yield. The consistency of these responses across diverse germplasms has suggested that a large portion of phenotypic variability in NDF concentration of smooth brome grass is regulated by loci or chromosome blocks that also regulate forage yield. The results of this study suggest that PSRI is potentially a better selection criterion than NDF, because the negative genetic correlation of PSRI with forage yield is weaker, less consistent, and more genetically pliable than the positive genetic correlation between NDF and forage yield. Responses of forage yield to divergent selection for PSRI all suggest that the genetic

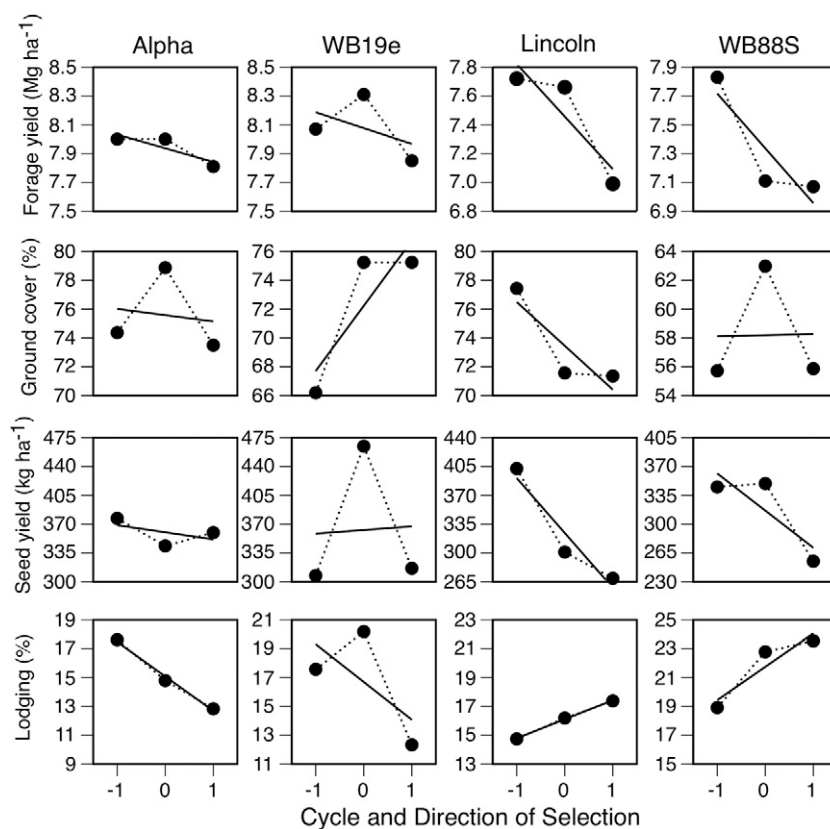


Figure 1. Means of four agricultural fitness traits measured on 12 smooth brome grass populations, created by one cycle of divergent selection for particle-size reduction index in four base populations (Cycle 0 of Alpha, WB19e, Lincoln, and WB88S, and their respective Cycle-1 high-PSRI and Cycle-1 low-PSRI progeny).

phenomena of linkage and drift are at least as important, or more so, than pleiotropy, a result diametrically opposed to observations following divergent selection for NDF. Furthermore, correlated selection responses for the other three variables also indicated that linkage and drift were more important than pleiotropy. Despite the optimism associated with these correlated selection responses, considerable care must be taken during selection for increased PSRI, due to the strong potential for undesirable responses in fitness traits, such as the changes observed for all four traits in WB88S of the current study. Because phenotypic selection for forage yield of spaced plants is generally not successful in smooth brome grass (Carpenter and Casler, 1990), combined selection for increased PSRI and forage yield (or minimally, maintenance of forage yield) should probably be conducted as progeny-test selection in which families are planted as sward plots (Casler, 2008) and harvested in a frequent-harvest system that would generate vegetative samples for PSRI analyses.

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